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Chapter

Papaya: The Versatile Tropical Fruit

Parichart Burns, Pimpilai Saengmanee and Uthaiwan Doung-ngern

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Abstract

Papaya (*Carica papaya L*) is a versatile tropical fruit with its usage ranging from consumption, cosmetics, to pharmaceuticals. In 2020, it was the third most-produced tropical fruit crop in the world. Papaya is a trioecious herbaceous plant with distinct flower and fruit morphological appearances. The fruits from hermaphrodite papaya are favorable for both consumption and processing due to their superior quality. Papaya has a genome size of 372 Mb and chromosome of 2n =18. The male and hermaphrodite papaya have XY and XYh sex chromosomes, respectively, while the female has XX. Using omics and bioinformatics approaches, papaya cultivars with desired fruit quality can be selected and identified from germplasm for incorporation in breeding programs. Papaya production can be done either in open fields or under protected cultivation. Open field cultivation provides for large-scale production, but with the disadvantages of variability in fruit yield, quality, and limitations on growing and harvesting seasons. Under protected cultivation, papaya can be cultivated in all seasons, whilst delivering higher yields. Conversely, multidisciplinary approaches with selected papaya cultivars, good farm management, and suitable conditions provide high yields of quality fruit for both consumption and processing, whilst minimizing the adverse effects related to environmental conditions.

Keywords: Papaya, *Carica*, Y-chromosome, PRSV, tropical fruit, cultivation, nutraceuticals

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1. Introduction

Papaya (*Carica papaya* L) is a tall herbaceous plant native to the Americas, specifically Mexico, Central America, and tropical areas of South America regions [1, 2]. Indigenous people have known of papaya and managed its cultivation since pre-Columbus times [3]. Papaya fruit, leaves, seeds, and sap have all been utilized widely as food, food additives including papain, and packaging for cosmetics. Although there are no remnants of papaya tissue in the archaeological record, analysis of 497 indigenous plant species databases confirm that papaya was one of the food sources for Mayans [4]. Following Spanish contact with central and south America, papaya was gradually introduced to Africa, South Pacific Islands, and the rest of the world as fruit [5, 6]. Presently, it is found in tropical and sub-tropical regions around the world. Green papaya fruit, young leaves, and shoots are used in many traditional Asian dishes, including those in India, Malaysia, Indonesia, and Thailand, and are consumed either fresh or cooked [7–9].

Countries	Plantation area (Ha)	Production (Tones)
India	142,000	6,011,000
Dominican Republic	12,395	1,271,303
Brazil	28,450	1,235,003
Mexico	18,983	1,117,437
Indonesia	11,404	1,016,388
Nigeria	92,338	877,120
Democratic Republic of the Congo	12,404	210,000
Colombia	7,309	194,332
Peru	12,359	186,508
Thailand	4,234	164,360

Table 1.
Top ten papaya production countries in 2020 [10].

Countries	Import value (US$)
United States	$134.2M
Germany	$33.3M
Portugal	$24.9M
Canada	$23.0M
Netherlands	$15.2M
Spain	$14.8M
France	$12.5M
United Kingdom	$11.6M
Singapore	$9.1M
Italy	$7.2M

Table 2.
Top ten papaya importers in 2020 by value [10].

In 2020, papaya was ranked the third most-produced tropical fruit crop in the world [10]. The major producing countries include India, the Dominican Republic, Brazil, Mexico, and Indonesia (**Table 1**). Papaya is also a highly traded fruit on international markets in fresh and processed form with the major importers being the USA, Germany, and Portugal (**Table 2**) [10].

2. Classification

Papaya is a member of the Family Caricaceae of which there are six genera *Carica*, *Jarilla*, *Horovitzia*, *Jacaratia*, *Vasconcella*, and *Cylicomorpha*. Papaya is a member of the Genus *Carica* of which there is only one species, *Carica papaya*. There are a total of 35 species in the Family Caricaceae; *Carica* (one), *Jarilla* (three), *Horovitzia* (one), *Jacaratia* (eight), *Vasconcella* (20), and *Cylicomorpha* (two). Although papaya is the only well-known edible fruit, other genera such as *Vasconcellea* (also called mountain papaya), *Jarilla* and *Jacaratia* are also consumed as fruit in Central America [3]. With the exception of the Genus *Cylicomorpha* which is native to Africa, all are native to the Americas.

2.1 Morphology and general characters

Plants in the family Caricaceae are stout-stemmed trees and exudate latex-like substances. Their leaves are palmately compound or lobed. The inflorescences are axillary and cymose and the flowers usually have fused petals. The fruits consist of numerous seeds surrounded by mucilage [11]. Of all the species in the family Caricaceae, papaya (*Carica papaya*) is the most well-known species ostensibly due to its fruit. Papaya is known by various names including pawpaw (Australia), Malagor (Thailand), tree melon (Brazil), and Fruitabomba (Cuba) [12]. Papaya is a herbaceous plant and, depending on the variety of which there are many, grows to a height of up to ten meters in height. The leaves are palmately-lobed with long and hollow petioles and the blades are divided into 5–9 segments. The flower buds are developed at the axils of the leaves. The fertilized fruit consists of up to 1000 seeds. The fruit skin is green at the unripened stage and turns yellow-orange when ripens. Generally, papaya plants have a life span of between five and ten years [13].

Most species in the family Caricaceae are dioecious. One is monoecious and two, *C. papaya* and *V. cundimarsensis* are trioecious [14]. Although the morphology of male, female and hermaphrodite papaya plants are very similar, their flowers and fruits were distinct. The male papaya plants produce small flowers in clusters with long peduncles and produce no or very small fruits. The female plants have large and round flowers while the fruits are round or ovule. The hermaphrodite flowers are cylindrical and produce cylindrical fruits. The fruits from hermaphrodite papaya have superior quality (size, shape, and flesh thickness) than those from female papaya plants. Based on fruit types, papaya cultivars can be divided into Solo and Formosa types. The fruits from the Solo group are small (500–700 g) with oval or pear shape, while those of the Formosa group are medium to large (≥1000 g) with cylindrical shape [15].

2.2 Genomics

Papaya (*Carica papaya*) has a relatively small genome of approximately 372 Mb across 18 chromosomes (2n = 2x = 18). Papaya chromosomes consist of autosomes and sex chromosomes. Male papaya has the sex chromosome XY and female XX, while the hermaphrodite papaya has XY^h. The nucleotide composition of the papaya genome is typical of dicot plants with a GC content of 36.51% GC and AT content of 63.49% [16]. The draft genomic sequence of a genetically modified variety of the female papaya, "SunUp", which was derived from the Hawaiian inbred cultivar "Sunset", was published in 2008 [17].

2.2.1 Sex determination

The papaya Y-chromosome deviated from the X-chromosome through deletions. Male-specific regions accounted for approximately 13% of Y-chromosome and share 99.6% of identity in male (MSY) and hermaphrodite (HSY) papaya [18, 19]. It consists of four knobs like heterochromatic structure and is heavily methylated

[18]. Expression of genes linked to X, Y and Yh chromosomes showed evidence of partial dosage compensation in X-link loci and a candidate gene associated with papaya sex determination and the transition to hermaphroditism, a homolog of the MADS-box protein short vegetative phase (SVG) [20, 21]. The dosage compensation of gene expression in papaya sex chromosomes was investigated further in female and male papaya and found to be at a gene by gene level. In addition, expression of most X-hemizygous genes was very low or none suggesting the role of gene silencing in controlling of transcriptional balance [22]. Recently, the landscapes of DNA methylation and transcriptomes were shown to be different in male and female papaya [23].

Using sequence information derived from papaya sex chromosomes, sex-specific primers were designed and used to screen plantlets/seedlings to identify fruit-bearing female and hermaphrodite types from males (MSY) [24]. More recently, a candidate gene, monodehydroascorbate reductase 4 (MDAR4), was identified from H-TSS No.7 line with X-chromosome mutant (3 bp deletion) resulting in all hermaphrodite progeny. MDAR4 is involved in a hydrogen peroxide scavenging pathway [25]. The marker developed from this gene has potential applications in papaya breeding, selection of potential lines for in vitro clonal propagation, and the production of high-quality commercial varieties of papaya seedlings.

2.3 Agronomic characteristics

Target genes related to papaya's important agronomic traits, including tolerance/resistance to abiotic and biotic stresses and fruit quality, were explored through omics and bioinformatics [26]. The papaya genome includes NBS genes which are disease-resistant genes with nucleotide-binding site motifs in the Toll/interleukin-1 receptor (TIR) and non-TIR subclasses [27]. Transcriptome profiles in young leaves of papaya ringspot virus (PRSV) resistant genetically modified variety "Sunup" showed high expression of several transcription factors (TFs) including MYB, ERF, WRKY, NAC, transporter proteins, and hormone-related proteins compared to susceptible "Sunset" papaya plants [28]. Under mild drought stress, stress-responsive genes were differentially expressed in papaya tissues with genes related to cell cycle and DNA repair processes. These stress-responsive genes were up-regulated in papaya leaves and sap while genes related to hormone signaling and sucrose metabolism were up-regulated in roots. Under severe drought stress genes related to oxidation-reduction, abiotic stress responses, and hormone signaling were also found to be up-regulated in all tissues [29]. Drought tolerant papaya had more photosynthetic II (PSII) efficiency than susceptible papaya. Drought susceptible plants displayed greater leaf abscission, less turgid shoots, and lower plant growth than those of tolerant papaya. Molecular analysis identified six transcription factors including *CpHSF*, *CpMYB*, *CpNAC*, *CpNFY-A*, *CpERF*, and *CpWRKY* that were highly expressed in tolerant papaya [30]. These genes were reportedly also involved in drought tolerance in rice and maize [31, 32]. Two transcription factors, RAP2.4 and DREB2 belonging to the ethylene response AP2/ERF family, have also been linked to extreme temperature responses in papaya. Overexpression of these genes in transformed tobaccos resulted in the cold (4°C) and heat tolerance (40°C) [33, 34]. In the regulation of fruit development and ripening, the papaya SQUAMOSA promoter binding protein Cp-SPL was found to be differentially expressed and cpmiRNA156 appears to play a critical role [35]. While in the carotenoid biosynthetic pathway, critical in the color development of papaya fruit, transcription factors HLH1 and HLH2 appear to regulate the transcription of lycopene β-cyclase genes [36].

3. Papaya responses to environment stresses

Environmental factors including soil, temperature, and water availability are external factors that significantly impact plant growth and development. The increased demand for papaya fruit as a source of food and plant-derived products and the marginalization of land available for cultivation due to increased housing needs has pushed papaya cultivation to less productive farms or in more developed countries, expensive protective housing cultivation. Further, climate change involving prolonged periods of adverse temperatures and extremes in weather patterns are contributing to the environmental stresses on papaya cultivation. These changes are further limiting not just the productivity, but also the zones of cultivation. Traditional cultivation areas are realizing significant reductions in yield or are forced to grow alternative crops. Papaya plants have optimal cultivation temperatures of between 25°C and 30°C. Temperature, moisture, light, and wind are also major environmental factors impacting papaya production [37, 38]. Temperatures lower than 16°C and higher than 36°C for extended periods negatively impact plant growth [39]. Under these climate extremes, different plant tissue types and organs, including roots, leaves, flowers, and fruit, exhibit variations in responses [40]. The use of traditional genotypes with desired plant fitness and plant developmental stages, fruit types, and yields are being negatively impacted pushing papaya breeding programs to develop varieties that are more adaptable and stable to seasonal changes [41].

In one study, the performance of a number of papaya cultivars including Solo, Formosa, and local commercial hybrids over two harvest seasons was compared. The results indicated that the summer harvest season with average temperatures of 24.9°C and maximums of 34.2°C were more productive than winter harvests where the average temperature was 21.9°C and the minimum 13.4°C [42]. Under low temperatures (<11°C), papaya plants produced fewer new leaves with no fruit set [43]. The optimal temperature for germination of papaya pollen was between 20 and 25°C at 72–80% humidity [44]. Further, extreme temperatures below 15°C and above 30°C negatively impacted germination with rates dropping to between 0 and 56%. Upon applying heat stress to papaya plants, it was shown that plants recovered from mild (37–41°C) and moderate (46°C), but not severe (49°C) heat stress. Photosynthesis was delayed while stress volatile production was induced [45].

Water stress has also been demonstrated to negatively impact papaya growth and development. For short periods of water stress, papaya leaves become droopy. If the water shortage continues, papaya plants will drop flower buds, and delay new fruit, flower, and leaf production. Water stress also results in leaf water potential and a reduction of stomatal opening. This, in turn, reduces carbon dioxide availability and consequently photosynthesis [46]. As a result of limited water availability, seed germination in many papaya cultivars is also delayed [47]. The genotype "Golden" papaya with less chlorophyll content outperformed high chlorophyll "Alianca" papaya under limited water availability [48]. Drought tolerant papaya was shown to have greater photosynthetic II (PSII) efficiency than susceptible ones. Susceptible plants displayed greater leaf abscission, less turgid shoots, and lower plant growth than those of more tolerant ones [30].

4. Papaya production

Papaya can be grown from seeds and vegetative tissues such as cuttings, grafting, and in vitro culture. The somatic embryos and somatic tissues can also be micro-propagated [49]. In many countries including India, Bangladesh, and Malawi papaya seeds are collected by growers from open-pollinated varieties of both female and hermaphrodite types and cultivated with little or no fertilization, irrigation, insect, or pathogen control. As a result, the yield and quality generally are variable as too the phenotype. Fruits are harvested and consumed within the household and are an important source of dietary fiber [50–52].

4.1 Open field

Commercial production of papaya is traditionally done under large open-field conditions. Selected cultivars, both inbred and hybrid varieties with the desired market characteristics of fruit color, weight, size, shape, and texture, are cultivated from seedlings. The plants are well maintained being fertigated, rouged to remove both off types as well as competing for vegetation, and sprayed with pesticides, fungicides, and other protective applications against insects and pathogens which negatively impact yield. Commercial papaya plantations are either rain-fed or irrigated by furrow, drip, sprinkler, or other mechanical means [53]. Integrated farm management has been practiced in some countries and has been shown to enhance papaya fruit yields and net return for growers even when compared to traditional management techniques [54]. Papaya fruit is harvested by hand using experienced pickers or, in some more developed countries, using mechanical harvesters. Fruit can be treated before packaging for long-distance transport. The use of cold room storage provides for the extended availability of fruit in the market and allows for farmers and wholesalers to also penetrate nontraditional markets and seasons offering significantly higher returns.

Large-scale open field conditions are the preferred cultivation for most papaya commercialization as it provides large-scale production with low to medium investment and operating costs. The drawbacks are less consistent fruit quality and yields as a result of seasonal variations and unexpected weather conditions such as flooding, in addition to physical damage to fruit as a result of environmental conditions, insects, and disease. Favorable cultivation conditions for papaya plants include cultivation temperatures of between 20°C and 30°C with a relative humidity of 66%, well-drained soil with a pH of between 6.0 and 6.5, low wind, adequate irrigation, and a balanced fertigation regime preferably via a drip irrigation system. Papaya plants are sensitive to frost with yields being negatively affected both through reduced temperatures and fruit quality. Generally, plants are productive after approximately nine months of transplanting and will yield for between two and four years, depending on the variety as well as weather conditions and inputs. Papaya is susceptible to a range of diseases and pests depending on the region. Papaya ringspot disease, caused by PRSV, is one of the most severe diseases and results in significant losses. Genetically modified PRSV resistant papaya varieties have been developed and have been found to be effective in controlling the disease [55]. Resistant varieties have been developed in a number of countries both on a research and commercial basis including the United States, Australia, Taiwan, China, India, Thailand, and The Philippines. In the United States two cultivars, Rainbow and SunUp, have been released on a commercial basis [56]. More recently, the use of gene mutation technologies, including CRISPR-Cas9, has allowed the mutation of cell receptors in papaya that facilitate cell infection by PRSV (as well in a range of potyvirus susceptible plants including species of *Capsicum*), thus rendering the mutated plant resistant.

4.2 Protected cultivation

Papaya production under protected conditions has been widely adopted using a variety of modifications applicable to local climatic conditions and cultivars used. The use of greenhouses with full climate control environments provides for year-round, high-quality fruit with maximum yields, albeit at very high capital input in addition to higher operating costs compared to open or protected field cultivation. In India, "Red Lady" papaya growing under greenhouse conditions performed well with reduced insect infestation and disease, and improved fruit quality [57, 58]. A combination of short stature cultivars and greenhouse conditions in Argentina and similar temperate regions allows for year-round papaya cultivation [59]. The use of closed plastic tunnels in the subtropical areas of Europe, including the Mediterranean and Canary Islands, has been successful in producing high yields. Similar methods have also been employed in Turkey where there is a widespread use of protected cultivation and greenhouses for a large range of crops [60]. A comparison of papaya cultivation and harvesting periods throughout the year indicated that greenhouse conditions result in the production of more uniform fruit quality in part due to a uniform season [61]. In southeastern Spain, five locally grown commercial papaya varieties were cultivated in multi-tunnel greenhouses covered with low-density polyethylene over fixed periods of 456 days and were considered a commercial success [62]. Under similar conditions and in the same region, five commercial cultivars of various geographic origins, have different plant and fruit types. Two varieties, "Siluet" and "Sensation", have been specially selected under greenhouse conditions and are both high yielding with the fruit of optimal quality for the European market including size, shape, weight, and importantly, total soluble solids (TSS), a major factor in determining sweetness. The greenhouses, with active climate control (ACC) incorporating both cooling and heating systems, enhanced "Siluet" papaya plant growth, flowering, fruit set, and yield resulting in doubling yields with both more and heavier fruit. Additionally, fruit quality factors including skin color, acidity, and TSS were not affected. Protected cultivation and the use of greenhouses offer an affordable and cost-effective strategy for papaya cultivation, especially in regions where open field cultivation, whether due to climate, soil, or other factors, is not feasible [63]. The compactness of the protected system producing large volumes of high quality, uniform fruit, aligned with readily available packaging and transport facilities lends itself to supplying both long and short distance high-value markets.

5. Nutraceuticals

Fruits, leaves, and seeds of papaya have a long history of human consumption and use. Fruit pulp is widely known for its nutritional value while the leaves and seeds are used in cooking in many cultures. Papaya pulp consists of macronutrients (protein, carbohydrate, lipid), fiber, minerals, carotenoids, and vitamins A, B, and C. Carotenoids from papaya are more bioavailable for human nutrition than those from tomato and carrot [64]. Other papaya tissues including leaves and seeds are of high nutrition, although with reduced levels of vitamins. Phytochemical analysis of papaya pulp reveals significant levels of phenols, terpenols, alkaloids, flavonoids, and saponins. Papaya leaves contain alkaloids, carpain, pseudocarpain and dehyrocarpaine, choline, carposide, saponins, pro-anthocyanin, benzyl isothiocyanate, while papaya seeds contain papaya oil, carpaine, benzyl isothiocyanate, benzyl glucosinolate, glucotropacolin, benzylthiourea, hentriacontane, and β-sitostrol. Papaya oil contains oleic acid (72.5%) and palmitic acid (12.5%) [49, 65]. Caffeic acid, myricetin, rutin, quercetin, α-tocopherol, benzyl isothiocyanate (BiTC), and kaempferol have been identified in papaya, all of which have antioxidant activities and in the plant either promote antioxidant enzyme expression or reduce reactive oxygen species (ROS) production [66]. Alkaloids, flavonoids, saponins, and oleic acid all poses anti-inflammatory activities [12, 67, 68]. Alkaloids, flavonoids, and saponins in papaya have been shown to inhibit the bacterial growth of *Enterobacter cloacae*, *Pseudomonas aeruginosa*, *Proteus vulgaris*, *Klebsiella pneumoniae*, and *Bacillus subtilis* [69–71]. Finally, papaya latex, often considered a nuisance and irritatant, has been shown to actively inhibits the growth of gram-negative bacteria [72].

6. Conclusions

Lifestyles in the twenty-first century (and beyond) are setting strikingly different needs and demands from those of earlier periods. Twenty-first century consumers have higher expectations with respect to fruit type and quality; more flavorful, of higher nutritional value with additional benefits to both health and to the environment. Growers are constantly under pressure in meeting not just the demand for quantity but, more importantly, quality and overall consumer satisfaction. With the ready availability of papaya genomics and transcriptome databases, desired agronomic characters associated with fruit quality, yield, and plant adaptation can be identified in germplasm and incorporated into breeding programs [73, 74]. Papaya can be produced "for all seasons" using open field cultivation under favorable conditions and in protected cultivation systems and climate-controlled greenhouses regardless of climate and region.

Papaya cultivation under open field conditions offers large-scale production with low to medium capital inputs and low operating expenses, offsetting the issues of inconsistent quality and quantity due to seasonal changes, disease, and abnormal weather events. Protected cultivation and greenhouses with controlled environments provide more expensive papaya fruit year-round, but in higher yields and into markets demanding higher quality and capable of absorbing the additional costs. These conditions provide flexibility for papaya production under varying conditions and locations.

Metabolites with nutritional values such as vitamin C and carotenoids in papaya can be consumed directly because of their high concentration in papaya flesh. Metabolites extracted from papaya fruit, including Papain, an enzyme widely known and used in the food industry and cosmetics, offer additional markets for the fruit. Other metabolites including antioxidants can be purified from papaya seed, flesh, and leaves and there are other active constituent molecules that are the subject of evaluation and many no doubt many others yet to be explored. With multiple applications and the potential for the increased demand for papaya fruit and products, papaya is undoubtedly the fruit for the future.

Conflict of interest

The authors declare no conflict of interest.

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